

Morphology and morphogenesis of the soil ciliate *Bakuella edaphoni* nov. spec. and revision of the genus *Bakuella* Agamaliiev & Alekperov, 1976 (Ciliophora, Hypotrichida)

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CONTENTS

Introduction	133
Materials, methods, and terminology	133
Description of <i>Bakuella edaphoni</i> nov. spec.	134
Revision of the genus <i>Bakuella</i> Agamaliiev & Alekperov, 1976	141
Key to species	141
Description of species	142
Unidentifiable taxa and species excluded from the genus <i>Bakuella</i>	144
Acknowledgements	147
References	147

SYNOPSIS. The morphology and morphogenesis of the hypotrichous ciliate *Bakuella edaphoni* nov. spec. from a soil in Qingdao, China, are described by observation of living and protargol impregnated specimens. The morphogenesis of cell division does not significantly differ from that of *B. salinarum*. *Bakuella* Agamaliiev & Alekperov, 1976 comprises 6 species: *B. marina* Agamaliiev & Alekperov, 1976 (type species), *B. crenata* Agamaliiev & Alekperov, 1976, *B. edaphoni* nov. spec., *B. kreuzkampii* nov. spec., *B. salinarum* Mihailowitsch & Wilbert, 1990, and *B. walibonensis* nov. spec. *Bakuella imbricata* Alekperov, 1982 and *B. polycirrata* Alekperov, 1988 are junior synonyms of *B. marina* and *B. crenata*, respectively. *Bakuella agamaliievi* Borror & Wicklow, 1983, *B. variabilis* Borror & Wicklow, 1983, and *B. pulchra* (Buitkamp, 1977) Jankowski, 1979, do not belong to the genus *Bakuella*. The obliquely arranged ventral rows behind the midventral cirri and the 3 enlarged frontal cirri could place the genera *Bakuella* and *Parabakuella* Song & Wilbert, 1988 in the subfamily Bakuellinae Jankowski, 1979, within the family Holostichidae Fauré-Fremiet, 1961.

INTRODUCTION

Agamaliiev & Alekperov (1976) established the genus *Bakuella* for two new hypotrichous ciliates with short, obliquely arranged cirral rows at the posterior end of the midventral row. Since then new representatives of this genus have been described by Alekperov (1982, 1988), Borror & Wicklow (1983), and Mihailowitsch & Wilbert (1990). A further new species is here described, the morphology and morphogenesis of which have been examined in detail. The genus *Bakuella*, which now contains 6 species from saline water, freshwater, and soil, is revised.

MATERIALS, METHODS, AND TERMINOLOGY

Bakuella edaphoni inhabits the upper soil layer (0–2 cm) on a hill in the city of Qingdao, China (36° 08' N; 120° 43' E). Excystation occurred about 3 days after the incubation of the air-dried soil was begun (for method see Buitkamp, 1977). Some individuals were taken from this initial culture and transferred to petri dishes containing Eau de Volvic as culture medium, with a few crushed wheat grains to promote bacterial growth.

The infraciliature was revealed by the protargol impregnation method according to Wilbert (1975). All counts and

measurements were made at a magnification of $\times 1500$. The drawings of the protargol impregnated specimens were made with a camera lucida. For clarity, in the morphogenic stages of *B. edaphoni*, the parental cirri are shown only by outline, whereas new ones are shaded. The terminology is according to Kahl (1932), Borrer (1972), Borrer & Wicklow (1983), Corliss (1979), Foissner (1982), and Hemberger (1982). Wiackowski (1985, 1988) designates both the zigzag arranged ventral cirri and the short rows posteriad of them as midventral cirri, which is correct in terms of morphogenesis. However, the term 'midventral row' is here used only for the sum of the zigzag arranged ventral cirri (= midventral cirri). The more or less obliquely arranged short rows are designated as ventral rows. For details of the morphometrical analysis see Berger et al. (1984).

DESCRIPTION OF *BAKUELLA EDAPHONI* NOV. SPEC.

DIAGNOSIS. *In vivo* 190–300 \times 50–85 μm . More than 100 macronuclear segments. 7 buccal cirri, 3 frontoterminal cirri, 8 transverse cirri, 9 pairs of midventral cirri, 7 ventral rows, and 39 adoral membranelles on average.

TYPE LOCALITY. Upper soil layer on a hill in the city of Qingdao, China.

TYPE MATERIAL. The slide of holotype specimens and 1 slide of paratype specimens are deposited in the collection of microscopic preparations of the College of Fisheries, Ocean University of Qingdao, China. 1 paratype slide (reference number 1990:11:19:1) is deposited in the Natural History Museum, London.

DESCRIPTION (Figs 1–5, Table 1). Long elliptical, posteriorly distinctly narrowed. About 2:1 dorsoventrally flattened, flexible. Macronuclear segments ellipsoidal, rather regularly distributed in cytoplasm. 2–7 (\bar{x} = 4.6, SD = 2.0, Vr = 43%, n = 16) micronuclei. Contractile vacuole at level of cytostome (Fig. 1). Cortical granules absent. Cytoplasm colourless, often densely packed with up to 5 μm large, colourless globules (mitochondria?), readily visible after protargol impregnation (Fig. 3). Feeds on bacteria, diatoms, zooflagellates, testaceans, and small ciliates. Moderately rapid movement.

Buccal area large. 1–7, usually 2 or 3, cirri immediately posterior to right frontal cirrus (Fig. 4, arrow). Midventral row terminates at about level of cytostome. Anterior ventral rows with 3–5 cirri, posterior rows with 7–14 cirri each. Both marginal rows terminate in median of cell without overlapping (Figs 1, 4).

COMPARISON WITH RELATED SPECIES. *Bakuella edaphoni* differs from the type species (Figs 21–35) in habitat and in that it has more buccal cirri and fewer frontoterminal cirri (Table 1). *Bakuella salinarum* has distinctly more pairs of midventral cirri and only 2 frontoterminal cirri (Fig. 41). In *B. kreuzkampii* and *B. walibonensis* the ventral rows are few in number and rather short (Figs 51, 52). Furthermore, both species have only 2 frontoterminal cirri. Recently, P. Eigner & W. Foissner (pers. comm. to H. Berger) found a rather similar terrestrial species which has, however, conspicuous cortical granules (visible *in vivo* and after protargol impregnation!) arranged in longitudinal rows. At superficial *in vivo*

Table 1 Morphometrical characterization of *Bakuella agamalievi* (aga, uncertain species, from Agamaliyev, 1972; wet silver impregnation), *B. crenata* (cre, from Agamaliyev & Alekperov, 1976; wet silver impregnation), *B. edaphoni* (eda, original data; protargol impregnation), *B. kreuzkampii* (kre, from Mihailowitsch & Wilbert, 1990; protargol impregnation), *B. marina* (ma1, from Agamaliyev & Alekperov, 1976; wet silver impregnation. ma2, original data of the population of Wilbert, 1986; protargol impregnation. ma3, *B. imbricata* from Alekperov, 1982; wet silver impregnation. ma4, original data; protargol impregnation), *B. salinarum* (sal, from Mihailowitsch & Wilbert, 1990; protargol impregnation), and *B. walibonensis* (wal, from Mihailowitsch & Wilbert, 1990; protargol impregnation). All measurements in μm . ? = sample size unknown; if only 1 value is known it is listed in column \bar{x} , if 2 values are available they are listed as Min and Max. Max = maximum value; Min = minimum value; n = number of individuals examined; SD = standard deviation; Vr = coefficient of variation in %; \bar{x} = arithmetic mean.

Character	Species	\bar{x}	SD	Vr	Min	Max	n
Body, length	aga	–	–	–	140	220	?
	cre	–	–	–	120	150	?
	eda	219.6	41.5	18.9	153	283	16
	kre	155.8	16.4	10.5	136	176	5
	ma1	–	–	–	120	140	?
	ma2	266.7	27.6	–	230	310	25
	ma3	–	–	–	110	130	?
	ma4	101.4	5.7	–	91	108	18
	sal	307.4	26.6	8.6	272	348	10
	wal	202.0	16.3	8.0	180	229	10
Body, width	eda	69.4	8.1	11.7	59	82	16
	kre	46.6	4.0	8.6	40	51	6
	ma2	85.0	14.8	–	70	110	11
	ma4	61.6	6.3	–	45	70	18
	sal	99.1	18.6	18.7	87	145	10
	wal	72.3	8.5	11.7	62	83	7
Adoral zone of membranelles, length	eda	62.8	10.9	17.4	47	82	16
Adoral membranelles, number	aga	–	–	–	25	30	?
	cre	–	–	–	28	30	?
	eda	38.9	2.8	7.3	34	45	16
	kre	33.7	2.3	6.8	30	37	7
	ma1	–	–	–	32	36	?
	ma2	40.4	4.2	–	34	51	25
	ma3	–	–	–	38	40	?
	ma4	32.4	2.4	–	28	36	12
	sal	55.4	5.1	9.2	47	63	10
	wal	39.2	4.1	10.5	33	47	17
Frontoterminal cirri, number	cre ¹	10.0	–	–	–	–	1
	eda	3.1	0.8	24.3	2	5	22
	kre	2.0	–	–	2	2	7
	ma1	9.0	–	–	–	–	?
	ma2	7.6	2.0	–	5	11	27
	ma3	9.0	–	–	–	–	?
	ma4	6.7	1.0	–	5	9	14
	sal	2.0	–	–	2	2	10
	wal	2.0	–	–	2	2	17
	Buccal cirri, number	cre	–	–	–	3	4
eda		7.4	1.3	17.7	5	9	24
kre		1.0	–	–	1	1	7
ma1		–	–	–	3	4	?
ma2		3.1	0.9	–	2	5	34
ma3		–	–	–	4	5	?
ma4		2.2	0.5	–	2	4	9
sal		7.1	0.9	12.3	6	8	10
wal		5.8	0.4	17.2	5	6	17

Character	Species	\bar{x}	SD	Vr	Min	Max	n	
Midventral row, number of pairs of cirri	aga	—	—	—	5	7?	?	
	cre ¹	5.0?	—	—	—	—	1	
	eda	9.5	2.3	24.1	5	14	24	
	ma1	12.0?	—	—	—	—	?	
	ma2	9.8	4.7	—	4	12	22	
	ma3	—	—	—	4	8	?	
	ma4	4.4	0.3	—	4	5	18	
	sal	26.0	7.9	30.4	22	38	7	
Number of ventral rows with 3 cirri	aga	13.8	0.4	3.0	13	14	15	
	cre ¹	3.0?	—	—	—	—	1	
	eda	2.6	1.0	37.0	1	5	22	
	kre	14.0	2.6	18.6	10	18	7	
	Number of ventral rows with more than 3 cirri	cre ¹	7.0	—	—	—	—	1
		eda	4.5	0.7	16.6	3	6	22
	Total number of ventral rows	cre ¹	10.0	—	—	—	—	1
		eda	7.1	1.3	18.1	5	10	22
kre		3.6	1.0	27.8	3	5	7	
ma1		10.0	—	—	—	—	?	
ma2		7.0	0.8	—	5	8	16	
ma3		—	—	—	5	7	?	
ma4		4.3	0.5	—	4	5	15	
sal		15.8	2.9	18.4	13	21	10	
Transverse cirri, number	wal	2.6	1.2	44.6	2	5	12	
	aga	5.0	—	—	—	—	?	
	cre ¹	7.0	—	—	—	—	1	
	eda	8.0	1.5	18.3	6	11	16	
	kre	5.3	1.0	18.9	5	7	7	
	ma1	10.0	—	—	—	—	?	
	ma2	7.0	1.6	—	5	11	27	
	ma3	7.0	—	—	—	—	?	
Right marginal row, number of cirri	ma4	7.2	1.4	—	5	9	20	
	sal	9.5	2.2	22.8	7	12	10	
	wal	5.2	0.7	13.1	4	6	15	
	aga	—	—	—	28	30	?	
	cre	—	—	—	40	45	?	
	eda	50.6	4.1	8.1	43	55	10	
	kre	41.0	5.2	12.7	34	46	6	
	ma1	—	—	—	55	60	?	
Left marginal row, number of cirri	ma2	44.4	7.6	—	34	63	23	
	ma3	—	—	—	40	42	?	
	ma4	40.7	5.6	—	34	54	9	
	sal	62.2	5.7	9.2	55	66	10	
	wal	60.5	6.3	10.4	51	66	11	
	aga	38.0	—	—	—	—	?	
	cre	—	—	—	38	40	?	
	eda	48.4	3.7	7.6	44	56	10	
Dorsal kineties, number	kre	37.6	4.5	12.0	30	40	7	
	ma1	—	—	—	52	56	?	
	ma2	35.9	9.0	—	23	53	23	
	ma3	—	—	—	32	35	?	
	ma4	28.3	2.7	—	25	33	9	
	sal	51.7	5.2	10.0	45	60	10	
	wal	51.5	4.5	8.8	42	50	13	
	cre ²	2.0?	—	—	—	—	?	
eda	3.0	0	0	3	3	24		
kre	3.0	0	0	3	3	7		
ma2	3.0	0	—	3	3	12		
ma3	3.0	—	—	—	—	?		
ma4	3.0	0	—	3	3	25		
sal	3.0	0	0	3	3	10		
wal	3.0	0	0	3	3	17		

¹ From Fig. 38.² See taxonomy of this species.

observation *B. edaphoni* can be easily confused with large *Holosticha* species (Foissner, 1982). The soil species *Paraurostyla pulchra* Buitkamp, 1977, which was probably erroneously transferred to the genus *Bakuella* by Jankowski (1979), almost certainly has no midventral cirri (Fig. 53).

MORPHOGENESIS OF CELL DIVISION (Figs 6–20).

The first event in morphogenesis is the formation of small groups of basal bodies close to the posterior end of the middle ventral rows (Fig. 6) and near the left transverse cirrus (Fig. 7, arrow). The basal bodies increase in number forming a longish field from which some migrate forward to the posterior portion of the midventral row (Fig. 8). The parental endoral membrane and the anterior third of the paroral membrane dedifferentiate (Fig. 8, small arrows). Simultaneously the posterior buccal cirri are modified to the anlage II of the proter (Fig. 8, large arrow). The pharyngeal fibres disappear. The macronuclear segments fuse to about 15 ellipsoidal segments with reorganization bands.

The adoral membranelles of the opisthe develop in a posteriad direction (Fig. 9, large arrow). At this stage some of the posterior cirri of the middle ventral rows are dedifferentiated and the posterior portion of the paroral membrane becomes disorganized. Between the dedifferentiated buccal row and the unaltered midventral row some small rows of basal bodies occur (Fig. 9, small arrows). The macronuclear segments differ in size.

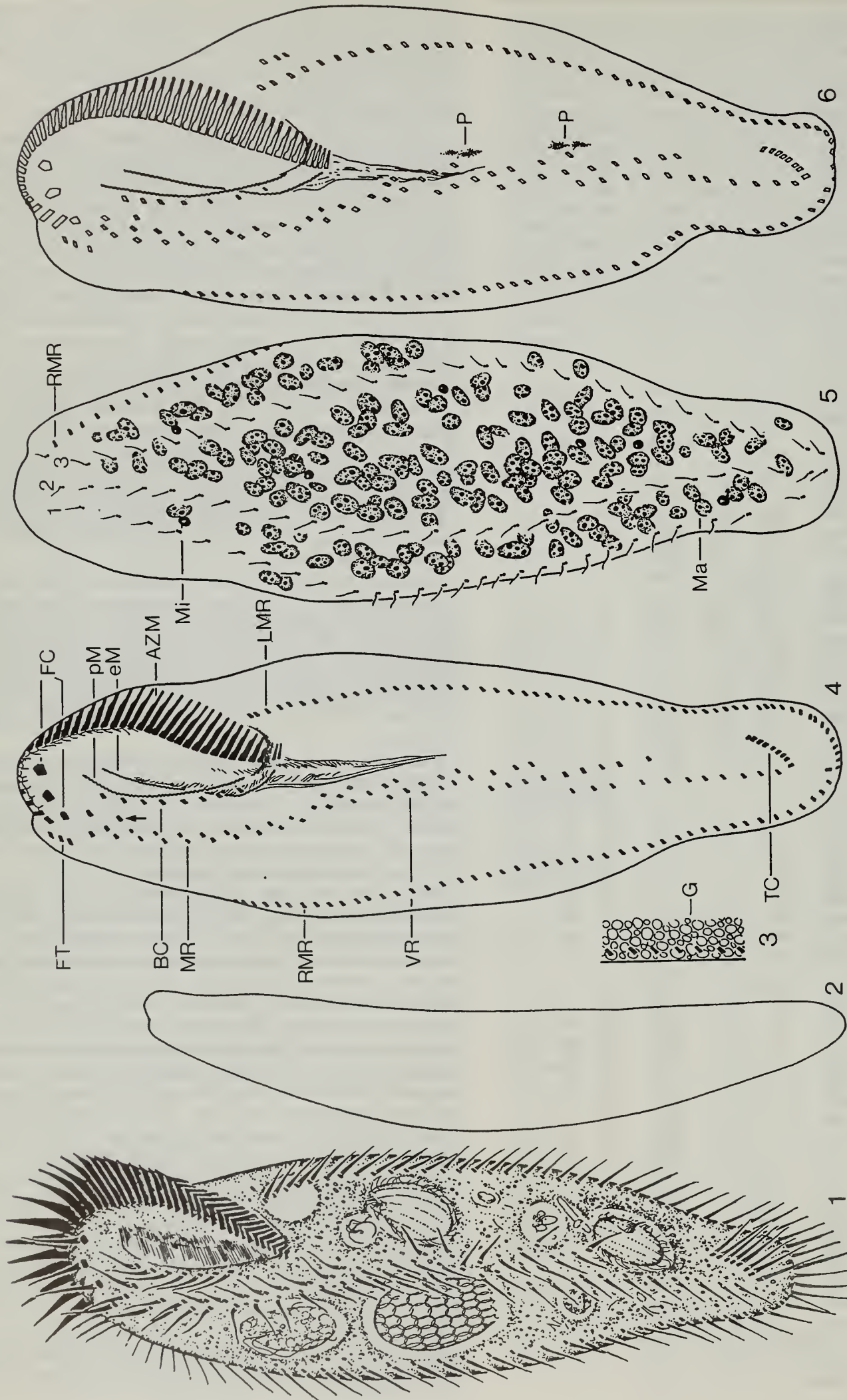
In the middle stages of morphogenesis most of the cirri of the ventral rows are modified to primordia of the opisthe. The parental buccal cirri are now a narrow band (Fig. 10, arrow). Some midventral cirri are obviously incorporated in the formation of the obliquely arranged primordial streaks. In both the marginal rows and in all dorsal kineties 2 primordia occur (Figs 10, 11). The macronucleus is a large single mass.

Somewhat later the proximal parental adoral membranelles begin with reorganization. Possibly the posterior end of the anlage I of the proter is involved in this process (Fig. 12, small arrow). Both in the proter and in the opisthe, about 20 short anlagen and the new left frontal cirrus (Fig. 12, large arrows) are recognizable.

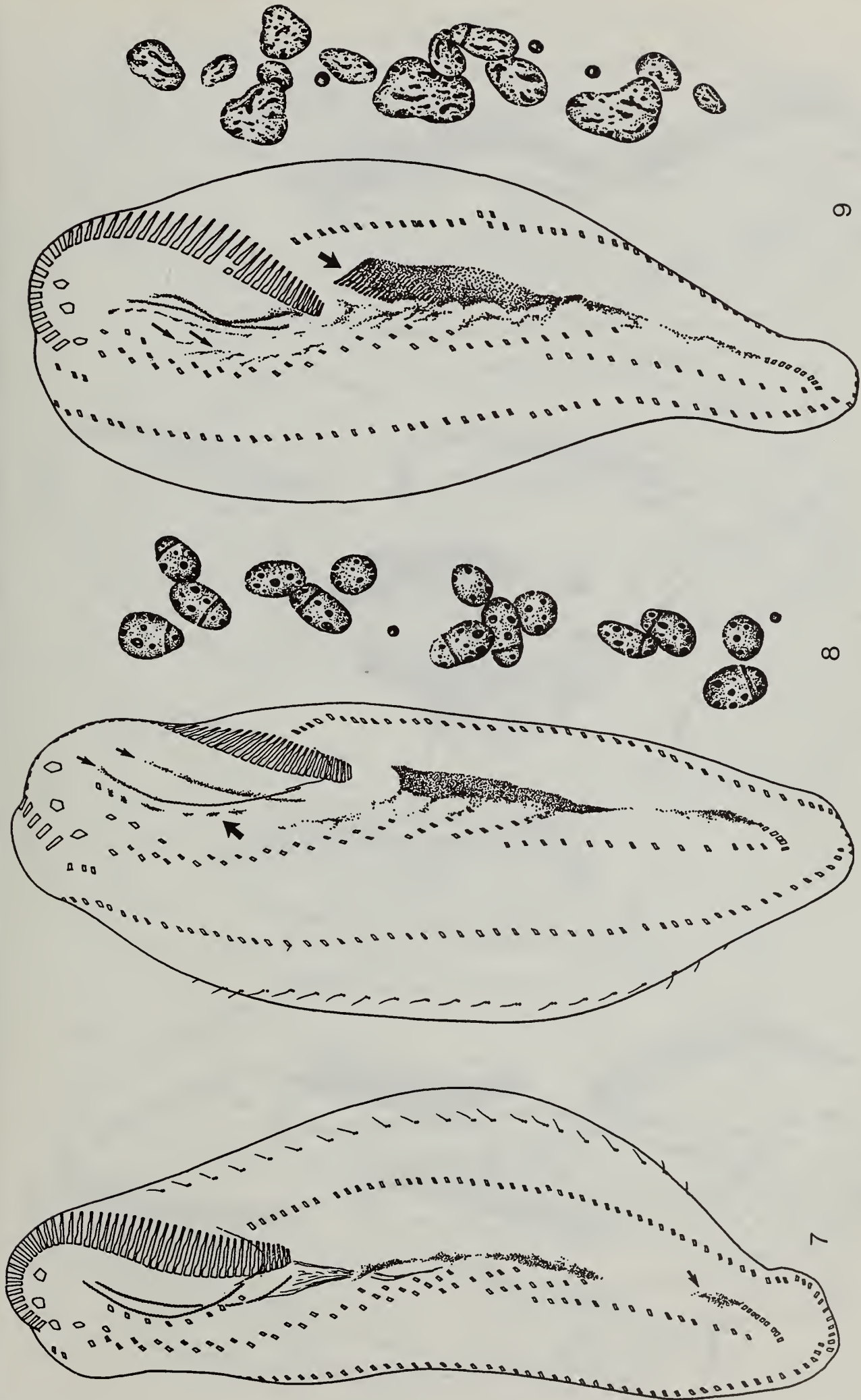
In the next stage the oral primordium of the opisthe is already distinctly bent to the right and completely modified to adoral membranelles (Fig. 13). The reorganization of the parental adoral zone of membranelles is restricted to about 10 proximal membranelles. In both the proter and the opisthe the numerous obliquely arranged streaks begin with the differentiation of cirri. The large arrows in Fig. 13 mark the penultimate streaks. These streaks appear to form the fronto-terminal cirri (Figs 13, 15) although this is unusual because, in general, the frontoterminal cirri originate from the anterior part of the posteriormost anlage. The morphogenesis of the dorsal infraciliature shows no peculiarities. The macronucleus and the micronuclei begin to divide (Fig. 14).

Figure 15 and 16 show a late morphogenetic stage. All new fronto-ventral-transverse cirri are differentiated and they begin to migrate to their final positions. Immediately before the separation of the proter and the opisthe, most of the parental cirri and dorsal kineties are resorbed (Figs 17, 18). The morphogenesis of the dorsal infraciliature shows unequivocally that no caudal cirri are present (Fig. 18).

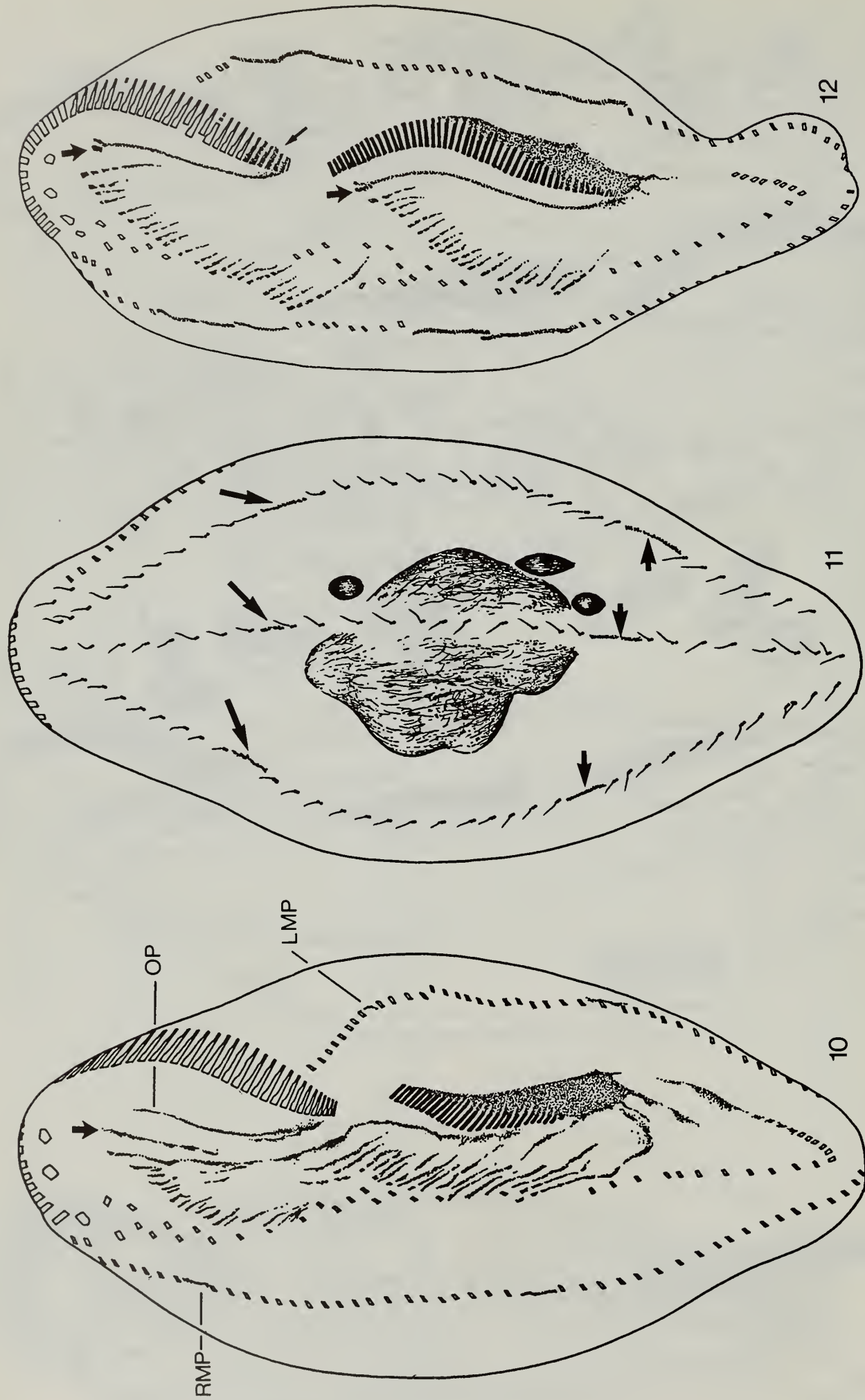
The postdividers have a wide elliptical outline (Figs 19, 20). Now the pharyngeal fibres impregnate again. The macronucleus commences with segmentation. In



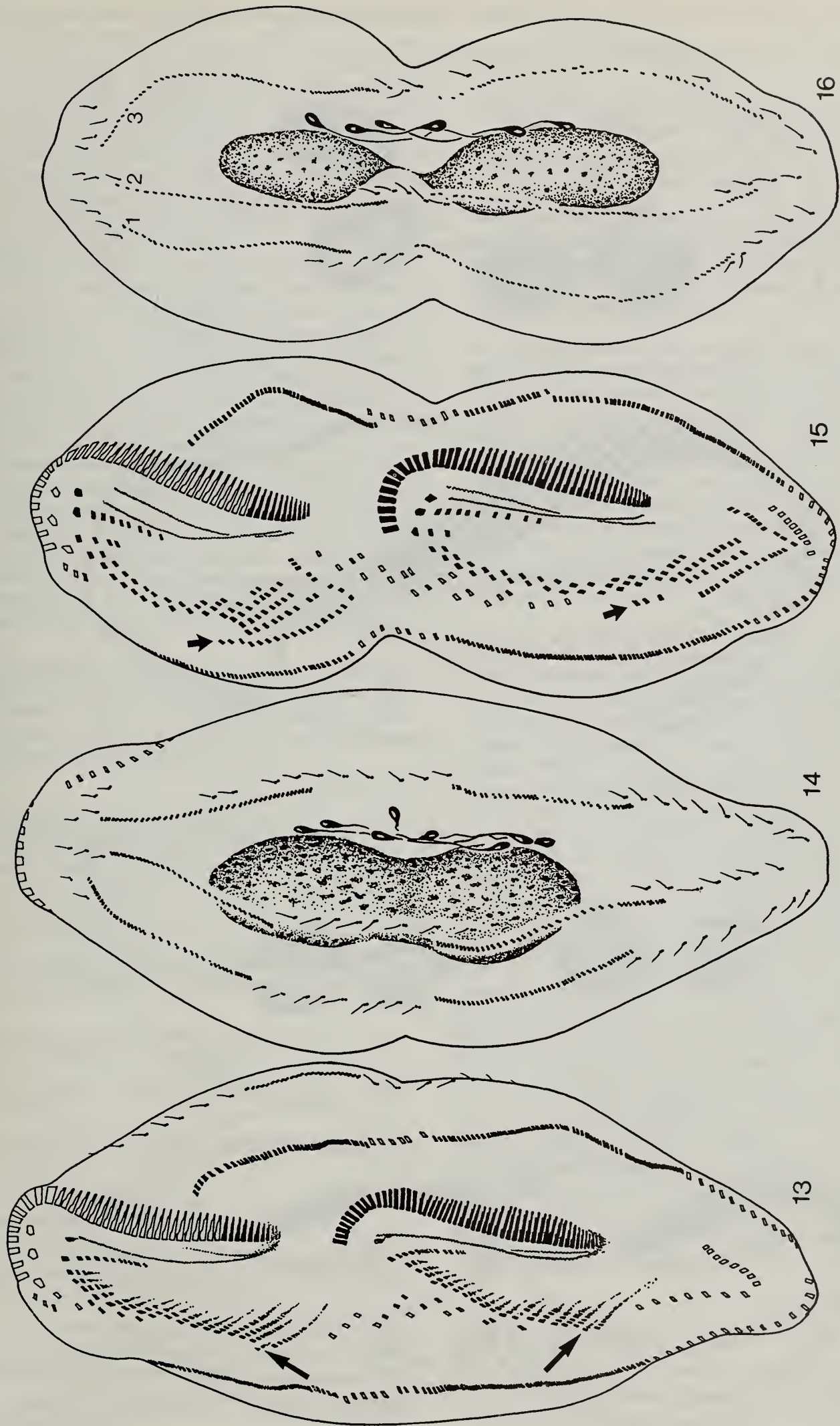
Figs 1-6 *Bakuella edaphoni* nov. spec. (1-6, originals. 1, 2, *in vivo*; 3-6, protargol impregnation). 1, 2 Ventral and lateral views, 225 μm , 215 μm . 3 Part of the pellicle to show the densely packed, up to 5 μm in diameter, globules (mitochondria?). 4, 5 Infraciliature in ventral and dorsal view, 240 μm . The arrow in Fig. 4 marks the cirri behind the right frontal cirrus. 6 Very early morphogenetic stage in ventral view, 280 μm . AZM = adoral zone of membranelles; BC = buccal cirri; eM = endoral membrane; FC = frontal cirri; FT = frontoterminal cirri; G = endoplasmic granule; LMR = left marginal row; Ma = macronuclear segment; Mi = micronucleus; MR = midventral row; P = oral primordium of the opisthe; pM = paroral membrane; RMR = right marginal row; TC = transverse cirri; VR = ventral rows behind the midventral row; 1-3 = dorsal kineties 1-3.



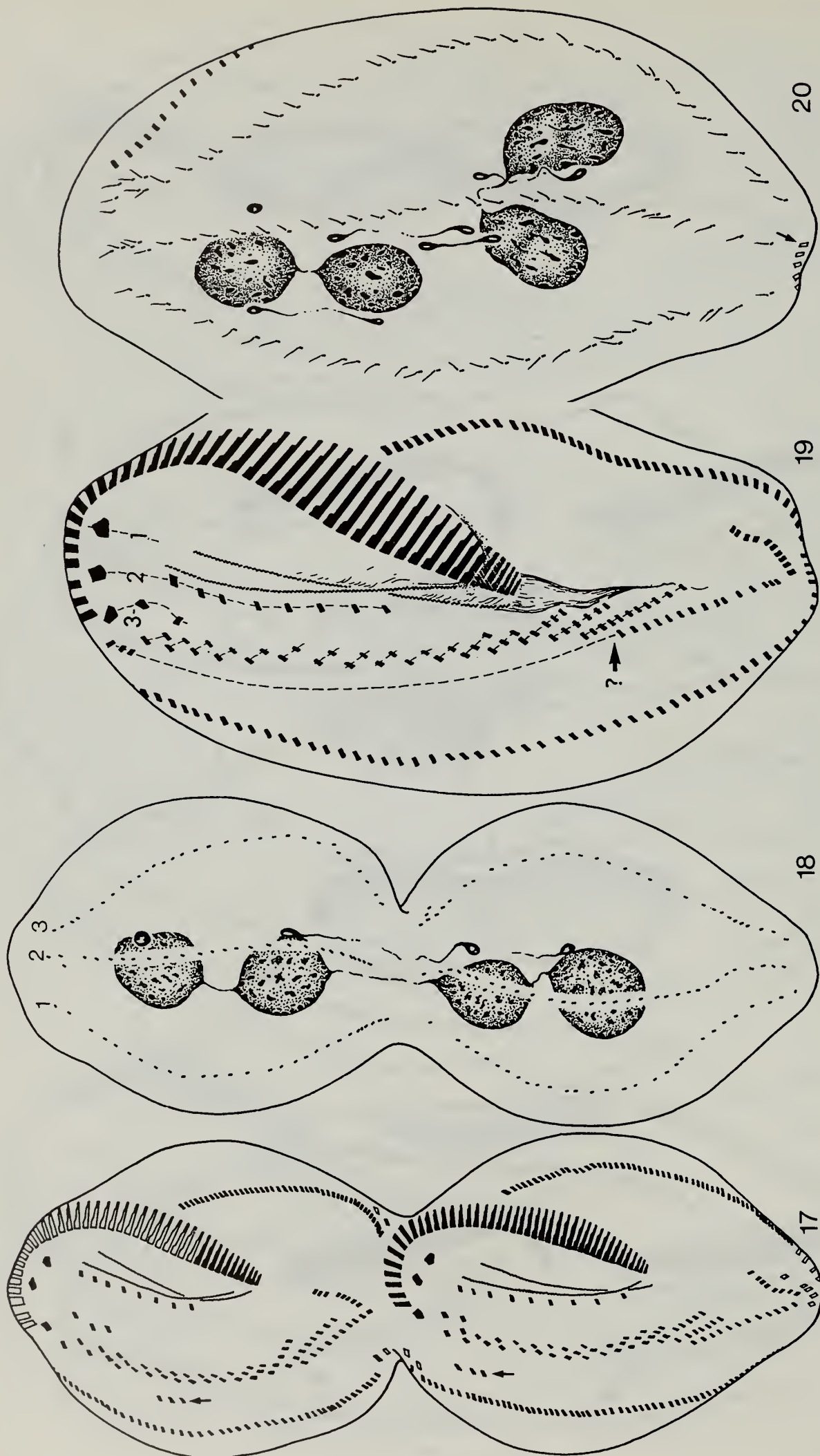
Figs 7-9 *Bakuella edaphoni* nov. spec. (7-9, originals. Morphogenetic stages in ventral view after protargol impregnation). 7 Very early stage, 275 μ m. The arrow marks the primordium close to the transverse cirri. 8 Early stage, 250 μ m. Small arrows, dedifferentiated endoral and paroral (only the anterior part) membrane; large arrow, dedifferentiated buccal cirri. 9 Early stage, 250 μ m. Large arrow, formation of the adoral membranelles of the opisthe; small arrows, primordia of the fronto-ventral-transverse streaks.



Figs 10-12 *Bakuella edaphoni* nov. spec. (10-12, originals. Morphogenetic stages after protargol impregnation). **10** Middle stage in ventral view, 200 μ m. Large arrow, anlage II of the proter. **11** Middle stage in dorsal view, 200 μ m. The arrows mark the primordia of the new dorsal kineties. **12** Middle stage in ventral view, 270 μ m. Large arrows, new left frontal cirrus of the proter and the opisthe; small arrow, reorganizing proximal part of the parental adoral zone of membranelles. LMP = primordium of the left marginal row; OP = anlage I of the proter; RMP = primordium of the right marginal row.



Figs 13-16 *Bakuella edaphoni* nov. spec. (13-16, originals. Morphogenetic stages after protargol impregnation). 13, 14 Middle stage in ventral and dorsal view, 220 μ m. Large arrows: anlagen of the frontoterminal cirri. 15, 16 Late stage in ventral and dorsal view, 205 μ m. Large arrows, new frontoterminal cirri. 1-3 = new dorsal kineties 1-3.



Figs 17-20 *Bakuella edaphoni* nov. spec. (17-20, originals. Morphogenetic stages after protargol impregnation). 17, 18 Very late stage in ventral and dorsal view, 220 μ m. The arrows mark the new frontoterminal cirri. 19, 20 Postdivisor in ventral and dorsal view, 120 μ m. The cirri which originate from the same anlage are connected by dotted lines; the origin of the frontoterminal cirri could not be precisely determined (arrow with ?; for details see text). The arrow in Fig. 20 marks the posterior end of the left marginal row. 1-3 = anlagen I, II, and III and dorsal kineties 1-3, respectively.

Figure 19 those cirri which originate from the same streak are connected by dotted lines.

DISCUSSION. The morphogenesis does not significantly differ from that of *B. salinarum* (Figs 41–50). Mihailowitsch & Wilbert (1990) describe a complete reorganization of the parental adoral zone of membranelles. This is, however, obviously a misinterpretation. Figs 46, 47 show that, just as in *B. edaphoni* and in *Keronella gracilis* Wiackowski, 1985, only the proximal membranelles are reorganized. Figure 45 does not show a morphogenetic stage as assumed by Mihailowitsch & Wilbert (1990), but a reorganizer.

The streaks (= anlagen) of the fronto-ventral-transverse primordia in the proter have the following origin: streak I, from the parental undulating membranes; it forms the new undulating membranes and the left frontal cirrus. Streak II, from the parental buccal cirri; it forms the middle frontal cirrus and the buccal cirri. Streak III, probably *de novo*; it forms the right frontal cirrus and 1 or more cirri behind this cirrus. Streaks IV to n, probably *de novo* and by modification of parental midventral cirri, respectively (Figs 9, 10); they form the numerous cirral pairs of the midventral row, the ventral rows, and the transverse cirri. The origin of the frontoterminal cirri could not be unequivocally recognized (Fig. 19, arrow with '?'). It gives the impression that they originate from the last but one streak which is, however, not in accordance with any other morphogenetic pattern of related species (Fig. 13). In the opisthe streaks I-n are derived from the oral primordium and modified ventral rows (Figs 8–10).

The morphogenesis of the dorsal infraciliature proceeds as in *B. salinarum* and e.g. in *Kahliella franzi* (Foissner, 1982) Berger & Foissner, 1988 or *Gonostomum strenua* (Engelmann, 1862) Sterki, 1878 (see Song, 1990), viz. according to type 1 of Foissner & Adam (1983).

REVISION OF THE GENUS BAKUELLA

Agamaliev & Alekperov, 1976

Bakuella Agamaliev & Alekperov, 1976

1976 *Bakuella* Agamaliev & Alekperov, Zool. Zh., 55: 128 – Type species (original designation): *Bakuella marina* Agamaliev & Alekperov, 1976.

1977 *Bakuella* Agam. & Alek. – Corliss, Trans. Am. microsc. Soc., 96: 137 (see nomenclature and taxonomy).

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Corliss, Ciliated protozoa, p. 309.

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Tuffrau, Trans. Am. microsc. Soc., 98: 526.

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Jankowski, Trudy zool. Inst., Leningr., 86: 50.

1979 *Bakuella* (*Bakuella*) Jankowski, Trudy zool. Inst., Leningr., 86: 50 – Type species (original designation): *Bakuella marina* Alekperov & Agamaliev, 1976.

1979 *Bakuella* (*Loxocineta*) Jankowski, Trudy zool. Inst., Leningr., 86: 51, 57 – Type species (original designation): *Bakuella crenata* Alekperov & Agamaliev, 1976.

1983 *Bakuella* Agamaliev & Alekperov, 1976 – Borrer & Wicklow, Acta Protozool., 22: 113.

1985 *Bakuella* – Small & Lynn, Phylum Ciliophora, p. 450.

1987 *Bakuella* Agamaliev & Alekperov, 1976 – Tuffrau, Anns Sci. nat., 8: 115.

1989 *Bakuella* Agamaliev et Alekperov 1976 – Alekperov, Ecology of marine and freshwater protozoans, p. 7.

1990 *Bakuella* Agamaliev & Alekperov, 1976 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 208.

DIAGNOSIS. Medium sized to large Holostichidae; obliquely arranged ventral rows situated behind midventral row; 3 slightly to distinctly enlarged frontal cirri; 2 or more frontoterminal cirri; transverse cirri present; 1 left and 1 right marginal row; caudal cirri absent.

ADDITIONAL CHARACTERS. Most of the species are described only from silver impregnated material. Thus the important character of the presence or absence of cortical granulation is unknown in these species. Outline usually long elliptical, both ends rounded. Body flexible. Adoral zone of membranelles 30–40% of body length. Undulating membranes bent and crossing. Bases of transverse cirri not conspicuously enlarged. 3 dorsal kineties (possibly a generic character; a redescription of *B. crenata* following protargol impregnation will probably reveal that it also has 3 dorsal kineties; Table 1). Dorsal cilia *in vivo* 3–5 µm long. Edaphic, limnic, and marine species.

REMARKS. Corliss (1977, p. 111, 137) erroneously designated *Bakuella* as a nomen nudum. The suggestion of Jankowski (1979) that the number of macronuclear segments should be used for the splitting into the 2 subgenera *Bakuella* and *Loxocineta* does not appear to be justified.

Three other genera are known which have obliquely arranged ventral rows behind the midventral row, viz. (i) *Parabakuella* Song & Wilbert, 1988 (3 frontal cirri; transverse cirri absent; 1 left and 1 right marginal row; caudal cirri present), (ii) *Keronella* Wiackowski, 1985 (many frontal cirri, i.e. the anterior part of the midventral row, form a 'bicornia'; transverse cirri present; 1 left and 1 right marginal row; caudal cirri present; see also Wirnsberger, 1987), and (iii) *Metabakuella* Alekperov, 1989 (many frontal cirri form a 'bicorna'; transverse cirri present; 1 [or more?] right and 2 or more left marginal rows; caudal cirri absent?). Two of these genera, viz. *Bakuella* and *Parabakuella*, can be united in the subfamily Bakuellinae Jankowski, 1979 for which we propose the following improved DIAGNOSIS: Holostichidae with more or less obliquely arranged ventral rows behind the midventral row; 3 more or less distinctly enlarged frontal cirri. TYPE GENUS: *Bakuella* Agamaliev & Alekperov, 1976. Nomenclatural remarks: Jankowski (1979, p. 74) established the family Bakuellidae. According to Article 50c (i) of the ICZN (1985) a change in rank of a taxon within the family group does not affect the authorship of the name of the taxon. Thus Jankowski is the author of the subfamily Bakuellinae and not Alekperov (1988), who erroneously wrote 'subfamily Bakuellinae (Jank.) comb. n.').

KEY TO SPECIES

- 1 Species from terrestrial habitats *B. edaphoni* (Figs 1–20)
 — Species from limnic or marine habitats 2

- 2 2 macronuclear segments *B. crenata* (Figs 36–40)
 — Many (usually >100) macronuclear segments (e.g. Fig. 22) . 3
 3 Posteriormost ventral row terminates roughly in the middle or at the end of the 2nd third of the cell; ventral rows with only about 3–4 cirri (Figs 51, 52) 4
 — Posteriormost ventral row terminates at about the level of the transverse cirri; ventral rows with up to 13 cirri (e.g. Figs 21, 41) 5
 4 1 buccal cirrus; an additional row between the anterior end of the midventral row and the right marginal row *B. kreuzkampii* (Fig. 52)
 — 5–6 buccal cirri; no such row *B. walibonensis* (Fig. 51)
 5 2 frontoterminal cirri; 22–38 pairs of cirri in the midventral row *B. salinarum* (Figs 41–50)
 — 5–11 frontoterminal cirri; 4–12 pairs of cirri in the midventral row *B. marina* (Figs 21–35)

DESCRIPTION OF SPECIES

REMARKS. Characters which are mentioned in (i) the diagnosis, (ii) the section 'additional characters' of the genus, (iii) the key, or (iv) the tables, are not repeated in the descriptions below. Thus, some of them are rather short.

Bakuella crenata Agamaliyev & Alekperov, 1976

1976 *Bakuella crenata* Agamaliyev & Alekperov, Zool. Zh., 55: 130 (Fig. 38).

1979 *Bakuella (Loxocineteta) crenata* – Jankowski, Trudy zool. Inst., Leningr., 86: 51.

1982 *Bakuella crenata* – Alekperov, Zool. Zh., 61: 1253.

1983 *Bakuella crenata* Agamaliyev & Alekperov, 1976 – Borrer & Wicklow, Acta Protozool., 22: 113.

1988 *Bakuella polycirrata* Alekperov, Zool. Zh., 67: 778 (nov. syn.; Figs 36, 37, 39, 40).

TAXONOMY. *Bakuella polycirrata* is almost certainly only a postdivider of *B. crenata* (Figs 36, 37). This is indicated by the enormous relative size of the adoral zone of membranelles (more than 50%), the unusual position of the porus of the contractile vacuole, and the immature ventral infraciliature (cp. Figs 19 and 36). The only significant difference is the number of dorsal kineties; only 2 in *B. crenata* and 5 in *B. polycirrata* (Fig. 37). This difference may be due to the wet silver impregnation method employed, which yields inaccurate data for the dorsal infraciliature (e.g., *Stylonychia mytilus* sensu Agamaliyev, 1978). Another possibility is that in Fig. 37 parental dorsal kineties are still preserved. A detailed redescription of this taxon is necessary.

MORPHOLOGY (Figs 36–40, Table 1). *In vivo* (?) up to 210 µm long. Each macronuclear segment with a micronucleus. Marginal rows distinctly separated posteriorly.

OCCURRENCE. Locus classicus is the Djeiranbatansky freshwater reservoir in Azerbaijan. *Bakuella polycirrata* was found in the same (?) freshwater habitat. Not found since.

Bakuella marina Agamaliyev & Alekperov, 1976

1976 *Bakuella marina* Agamaliyev & Alekperov, Zool. Zh., 55: 129 (Figs 21, 22).

1979 *Bakuella (Bakuella) marina* – Jankowski, Trudy zool. Inst., Leningr., 86: 50.

1982 *Bakuella marina* – Alekperov, Zool. Zh., 61: 1253 (Figs 26, 27).

1982 *Bakuella imbricata* Alekperov, Zool. Zh., 61: 1253 (nov. syn.; Figs 31, 32).

1983 *Bakuella marina* A. et A., 1976 – Borrer & Wicklow, Acta Protozool., 22: 113.

1983 *Bakuella marina* Agamaliyev et Alekperov, 1976 – Agamaliyev, Ciliates of Caspian Sea, p. 105.

1986 *Bakuella marina* Agamaliyev – Wilbert, Symposia Biologica Hungarica, 33: 251 (Figs 28–30).

NOMENCLATURE AND TAXONOMY. '*Bakyella marina*' in Agamaliyev (1976, p. 91) is an incorrect subsequent spelling. *Bakuella marina* is probably the senior synonym of *B. imbricata* because the important biometric data are rather similar (cp. Figs 21, 26, 31, Table 1). *Bakuella marina* sensu Wilbert (1986) is distinctly larger. Other characters, however, agree well, so that the identification can be accepted for the time being.

MORPHOLOGY (Figs 21–35, Table 1). *In vivo* (?) about 200 µm long. Contractile vacuole porus at level of cytostome (Figs 21, 23, 26). Posterior ventral rows with up to 13 cirri (Figs 21, 24, 26, 31). Marginal rows usually distinctly separated posteriorly. Sometimes with 4 dorsal kineties (Fig. 30).

OCCURRENCE AND ECOLOGY. Locus classicus is the Caspian Sea (see also Agamaliyev, 1976). Wilbert (1986) found it in saline lakes in Saskatchewan, Canada. According to Hammer (1986) *B. marina* occurs at salinities of 2–37%. Chaouite et al. (1990) recorded it in mineral and hot springs in France. Locus classicus of the synonymous *B. imbricata* is the Djeiranbatansky freshwater reservoir, Azerbaijan.

Bakuella salinarum Mihailowitsch & Wilbert, 1990

1990 *Bakuella salinarum* Mihailowitsch & Wilbert, Arch. Protistenk., 138: 208 (holotype slide deposited in Institut für Landwirtschaftliche Zoologie und Bienenkunde, University of Bonn, Germany).

MORPHOLOGY (Figs 41–50, Table 1). *In vivo* 280–350 µm long. Contractile vacuole roughly in middle of cell. 2 micronuclei. Cells brownish (no information is given why). 2 cirri situated behind right frontal cirrus. Anteriormost buccal cirrus slightly enlarged. Midventral row terminates slightly behind middle of cell. Ventral rows rather densely arranged. Marginal rows slightly overlapping. Very probably during morphogenesis the parental adoral zone of membranelles is reorganized only proximally and not completely as supposed by Mihailowitsch & Wilbert (1990; see discussion of *B. edaphoni*).

OCCURRENCE AND ECOLOGY. Locus classicus is a salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany (for details see Mihailowitsch, 1989). Feeds on bacteria. Mihailowitsch & Wilbert (1990) give the following autecological data (n = 28): 5.3–16.3 °C, pH 7.0–7.7, 19–187 mg l⁻¹ CO₂ (free), 2.2–9.6 mg l⁻¹ O₂, 0.13–7.3 mg l⁻¹ NH₄⁺-N, 0.02–0.4 mg l⁻¹



Figs 21–32 *Bakuella marina* (21, 22, from Agamaliev & Alekperov, 1976; 23, from Wilbert, 1986 slightly modified; 24, 25, originals of a population from a saline lake in Saskatchewan, Canada; 26, 27, 31, 32, from Alekperov, 1982; 28–30, from Wilbert, 1986. 21, 22, 26, 31, wet silver impregnation; 23–25, 28–30, protargol impregnation; 27, 32, Feulgen staining). 21–32 Infraciliature in ventral and dorsal view and nucleus apparatus, 21, 22 = 120 μm , 23–25 = 230–310 μm , 26, 27 = ? μm , 28 = 210 μm , 29 = 240 μm , 30 = 212 μm , 31, 32 = 110–130 μm .

NO_2^- -N, 0.63–10.6 mg l^{-1} NO_3^- -N, 300–12763 mg l^{-1} Cl^- , 216–3590 mS m^{-1} spec. conductivity.

***Bakuella walibonensis* nov. spec.**

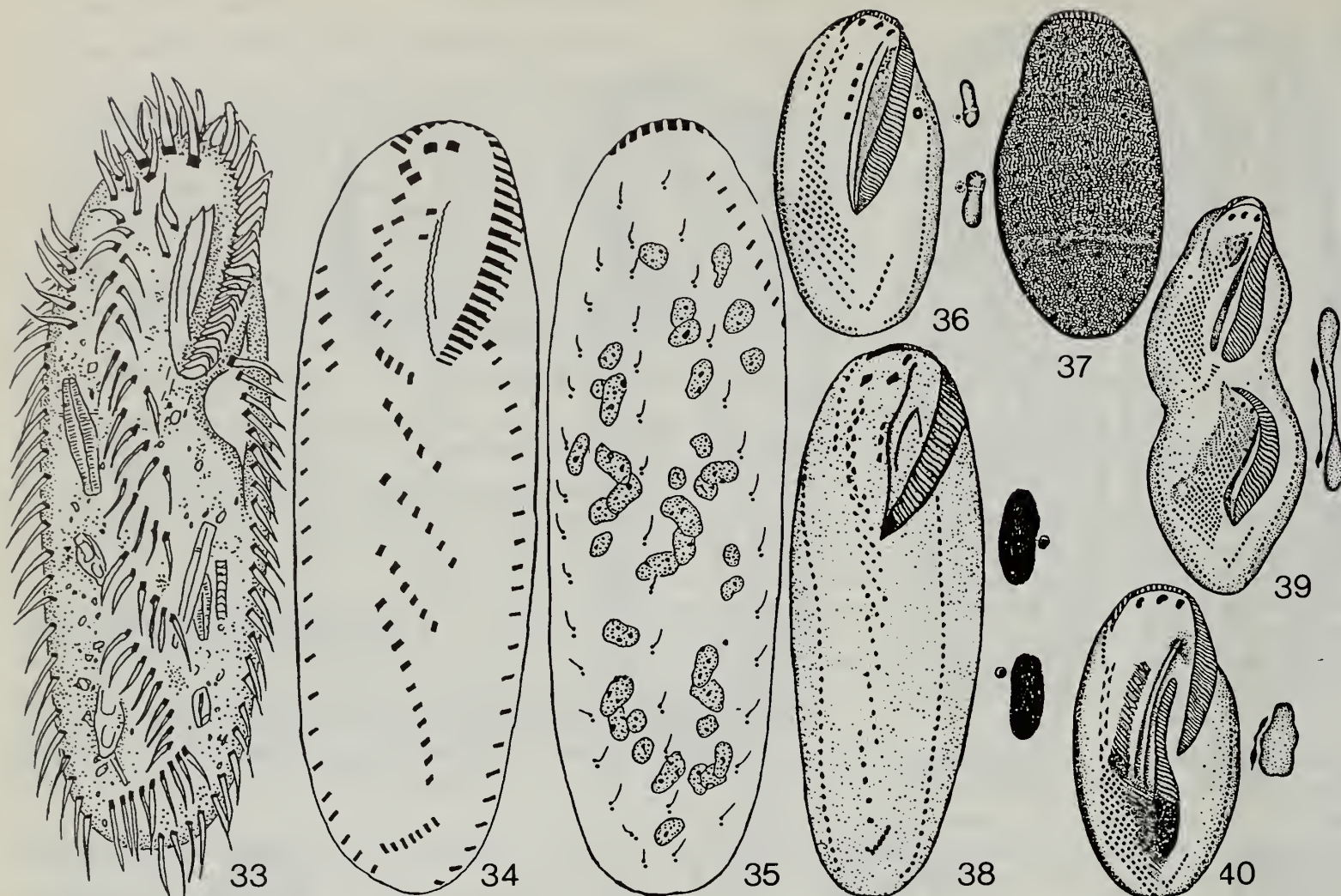
1990 *Bakuella* spec. 1 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 213.

TAXONOMY. Redescription necessary, especially *in vivo* observations. Differs from the rather similar *B. kreuzkampii* (Fig. 52) in that it has more buccal cirri and no additional 'frontal' row between the anterior end of the midventral row and the right marginal row.

DIAGNOSIS. After protargol impregnation about 180–230 \times 60–80 μm . More than 100 macronuclear segments. 6 buccal cirri, 5 transverse cirri, 14 pairs of midventral cirri, and 39 adoral membranelles on average. 2–5 ventral rows and consistently 2 frontoterminal cirri.

TYPE LOCALITY. Salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany.

MORPHOLOGY (Fig. 51, Table 1). Contractile vacuole situated slightly behind the middle of the cell. 3 cirri left of anterior end of midventral row. Ventral rows terminate at about level



Figs 33–35 *Bakuella marina* (originals of a population from a saline lake in Saskatchewan, Canada). 33 Ventral view *in vivo*. 34, 35 Infraciliature in ventral and dorsal view, protargol impregnation, 91–108 μm .

Figs 36–40 *Bakuella crenata* (36, 37, 39, 40, from Alekperov, 1988; 38, from Agamaliev & Alekperov, 1976. 36–40, wet silver impregnation; nuclear apparatus after Feulgen staining). 36, 37 Infraciliature of a postdivider in ventral and dorsal view, 66 μm . 38 Infraciliature in ventral view, 195 μm . 39 Late morphogenetic stage in ventral view. 40 Reorganizer in ventral view.

of contractile vacuole and marginal rows almost exactly in median of cell.

Bakuella kreuzkampii nov. spec.

1990 *Bakuella* spec. 2 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 213.

TAXONOMY. Redescription necessary, especially *in vivo* observations. The rather similar *B. walibonensis* has more buccal cirri and no cirral row between the anterior end of the midventral row and the right marginal row (Fig. 51).

DIAGNOSIS. After protargol impregnation about 135–175 \times 40–50 μm . More than 100 macronuclear segments. 5 transverse cirri, 14 pairs of midventral cirri, and 34 adoral membranelles on average. 3–5 ventral rows and consistently 1 buccal cirrus and 2 frontoterminal cirri.

TYPE LOCALITY. Salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany.

MORPHOLOGY (Fig. 52, Table 1). A short row with about 6

cirri between anterior end of right marginal row and midventral row. Ventral rows terminate at about level of contractile vacuole and marginal rows almost exactly in median of cell.

UNIDENTIFIABLE TAXA AND SPECIES EXCLUDED FROM THE GENUS *BAKUELLA*

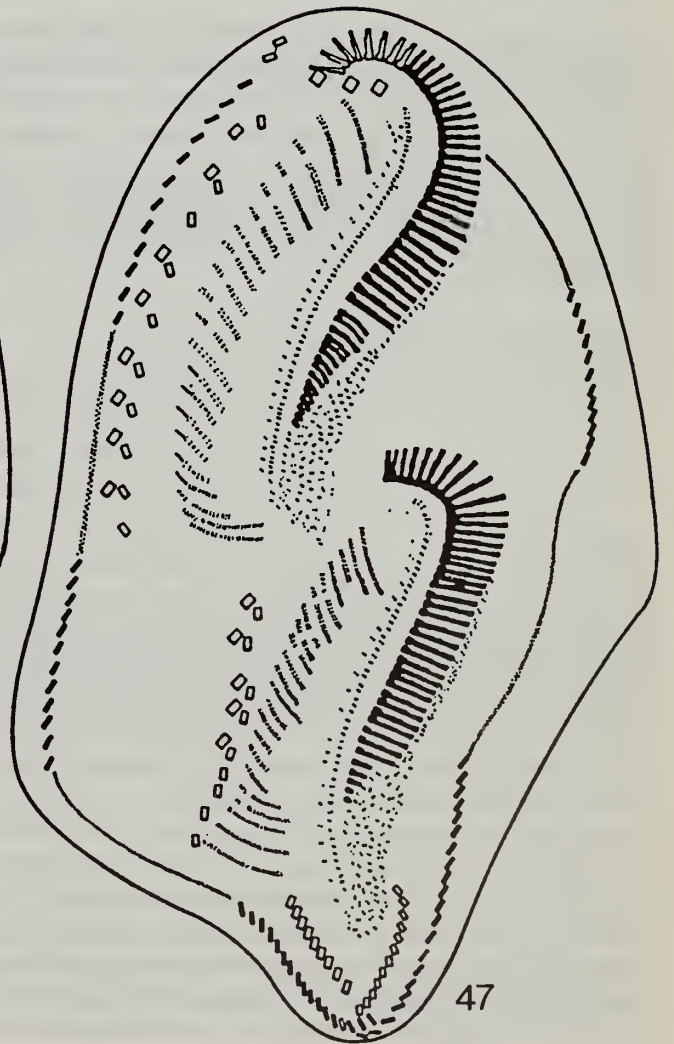
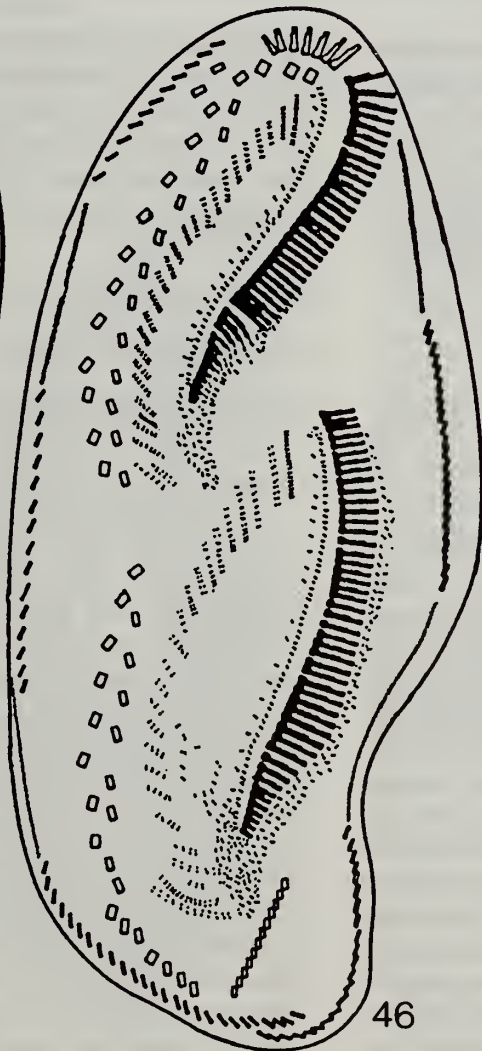
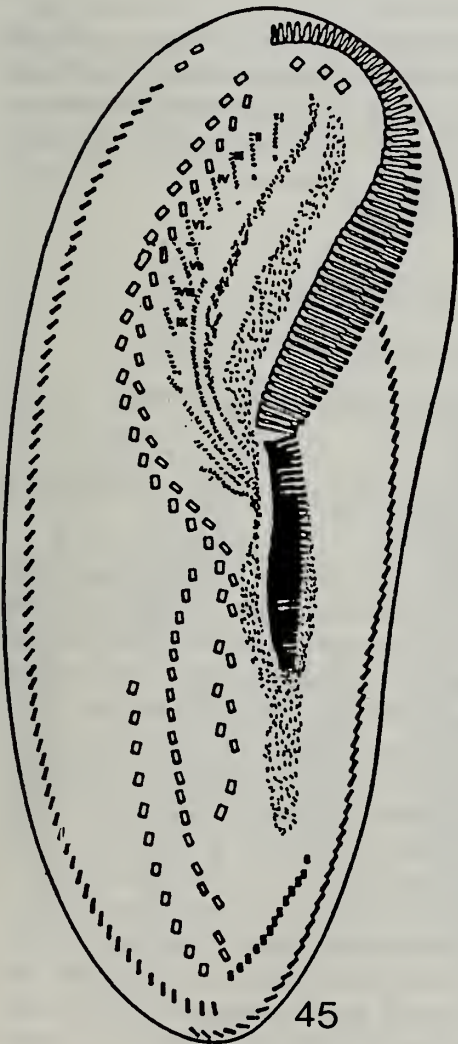
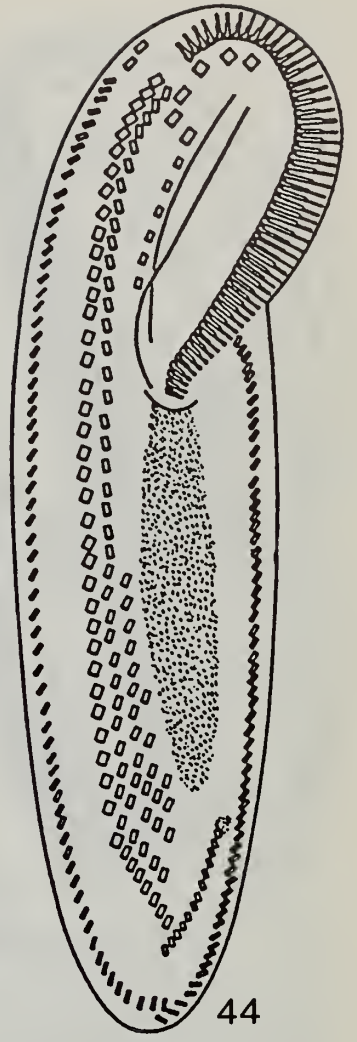
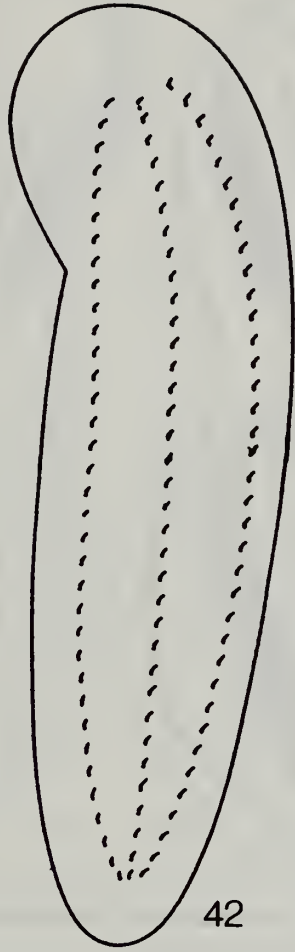
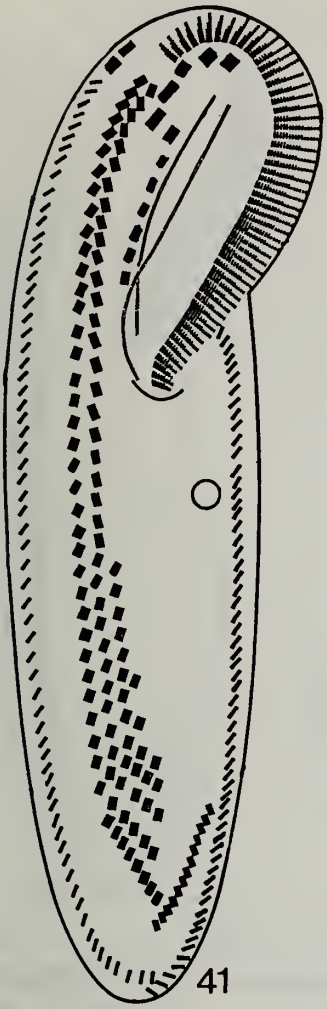
Bakuella agamalievi Borror & Wicklow, 1983

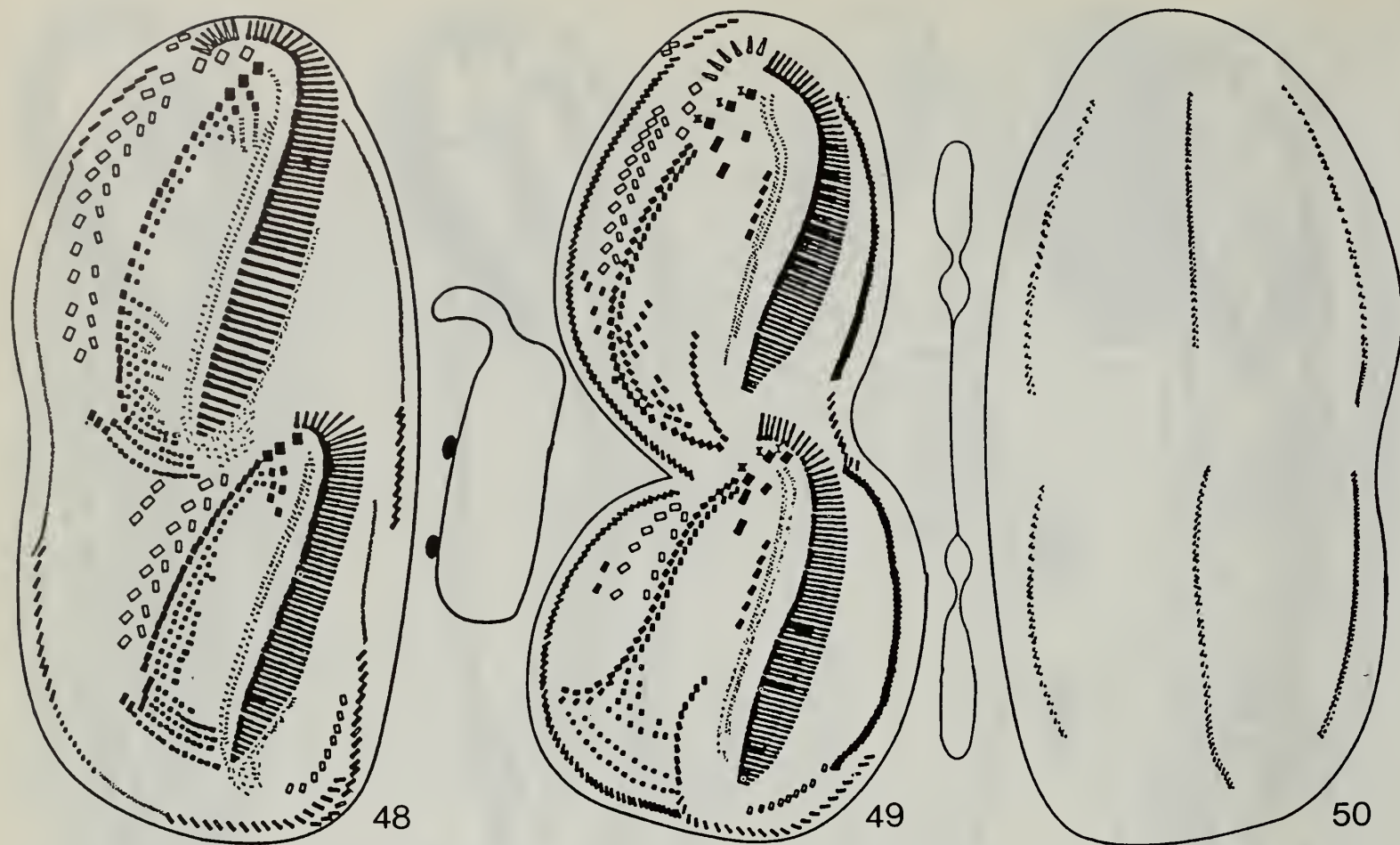
1972 *Holosticha manca* Kahl, 1932 – Agamaliev, Acta Protozool., 10: 21 (misidentification; Figs 54, 55).

1983 *Bakuella agamalievi* Borror & Wicklow, Acta Protozool., 22: 114, 117, 120.

REMARKS (Figs 54, 55, Table 1). This species was established for the rather superficially described *Holosticha manca* sensu Agamaliev (1972). Almost certainly *Keronopsis rubra* sensu Agamaliev (1974, p. 72, Fig. 10) represents the same taxon. Whilst in both descriptions buccal and frontoterminal

Figs 41–47 *Bakuella salinarum* (from Mihailowitsch & Wilbert, 1990. 41–47, protargol impregnation). 41, 42 Infraciliature of a non-dividing specimen in ventral and dorsal view, 225 μm . 43, 44 Very early and early morphogenetic stage in ventral view. 45 Reorganizer. 46, 47 Late stages in ventral view.





Figs 48–50 *Bakuella salinarum* (from Mihailowitsch & Wilbert, 1990. 48–50, morphogenetic stages after protargol impregnation). 48, 49 Late and very late stage in ventral view, 303 μm , 340 μm . 50 Late stage in dorsal view, 303 μm .

cirri are absent, it is assumed that they were overlooked, possibly due to the inappropriate wet silver impregnation method used. Because no ventral rows are recognizable, it must be excluded from *Bakuella*. Possibly it belongs to the genus *Holosticha*. Length about 2.5 times width. Both marginal rows terminate at level of transverse cirri. Number of dorsal kineties unknown. Locus classicus is the Caspian Sea. Not found since.

Paraurostyla pulchra Buitkamp, 1977

1977 *Paraurostyla pulchra* Buitkamp, Decheniana, 130: 119 (Fig. 53).

1979 *Bakuella pulchra* – Jankowski, Trudy zool. Inst., Leningr., 86: 83.

REMARKS (Fig. 53). '*Parayrostyla pulchra*' in Jankowski (1979, p. 83) is a misspelling. Its inclusion in the genus *Bakuella* is not justified, because it has no midventral row. However, there is no doubt that some other characters, such as the absence of caudal cirri, the 3 dorsal kineties, the large number of macronuclear segments, the short cirral row near the anterior end of the right marginal row which simulates the frontoterminal row, and more than 1 buccal cirrus, remind one of members of the genus *Bakuella*. Thus only a detailed redescription, including an investigation of the morphogenesis, will definitively elucidate the correct systematic position of *Paraurostyla pulchra*. Roughly spindle-shaped. Contractile vacuole slightly above middle of cell. 2 ventral cirri in front of transverse cirri, which are circa 18 μm long and only slightly enlarged. Right marginal row begins at about level of posterior buccal cirri and terminates at level of transverse cirri; left

marginal row terminates in median of cell. Feeds on diatoms and ciliates. Locus classicus of *P. pulchra* is the upper soil layer (0–5 cm) of a pasture near Bonn, Germany. Not found since. Buitkamp (1979) counted 79 individuals g^{-1} dry soil 6 days after incubation at 30°C. Biomass of 10^6 individuals about 300 mg (Foissner, 1987).

Bakuella variabilis Borror & Wicklow, 1983

1979 ?*Bakuella* sp. – Borror, J. Protozool., 26: 547 (Fig. 56).

1983 *Bakuella variabilis* Borror & Wicklow, Acta Protozool., 22: 111 (Fig. 57).

1989 *Metabakuella variabilis* (B. & W.) – Alekperov, Ecology of marine and freshwater protozoans, p. 7.

REMARKS. *Bakuella variabilis* has 2–5 left marginal rows. Furthermore, the ventral rows are rather long and are not obliquely arranged behind the midventral row as in all other species of the genus (Fig. 57). The arrangement of the ventral rows reminds strongly on *Urostyla grandis* Ehrenberg, 1830. *Urostyla*, however, has many frontal cirri which form a bicorona (see Foissner et al., 1991, Ganner, 1991). A classification in the genus *Metabakuella* is also uncertain, because the type species, *M. perbella* (Alekperov & Musayev, 1988) Alekperov, 1989, has a bicorona too. The correct generic classification of *B. variabilis* can only be determined after a detailed description of the morphogenesis. Possible it needs a genus of its own. *In vivo* 225–240 μm long. Flexible and opaque. More than 100 small macronuclear segments. Contractile vacuole at about the level of the cytostome. Cortical

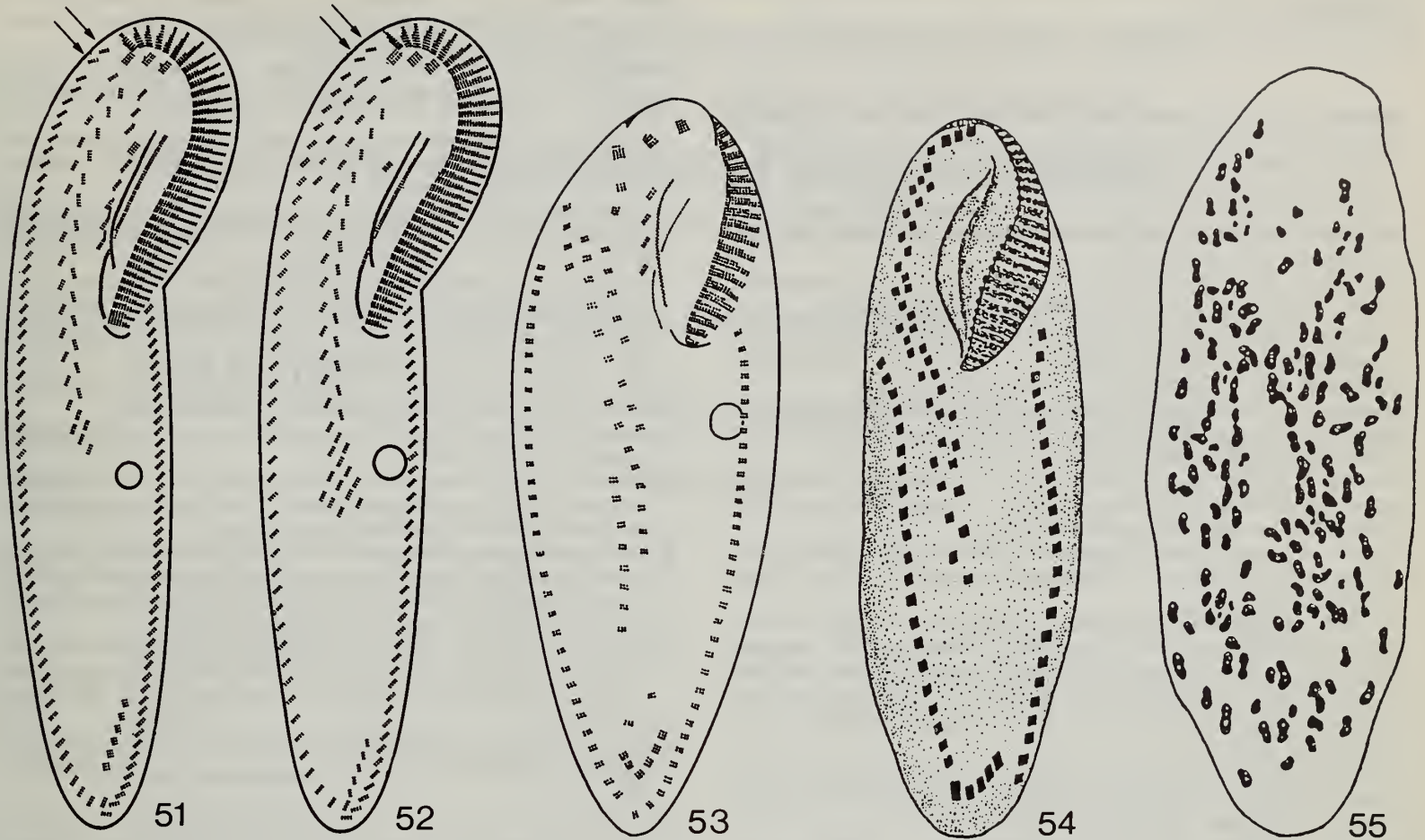
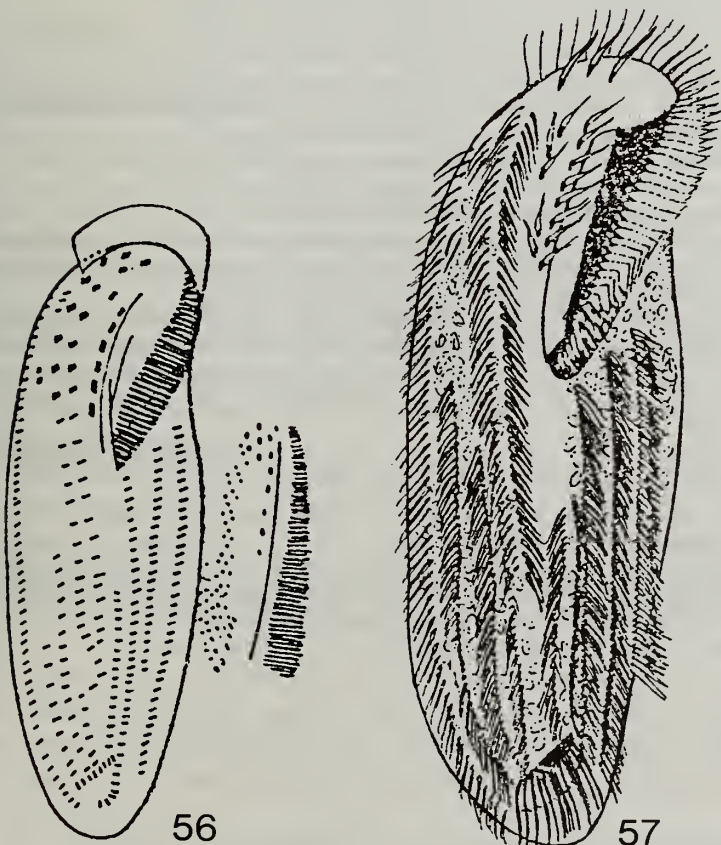


Fig. 51 *Bakuella walibonensis* nov. spec. (from Mihailowitsch & Wilbert, 1990). Infraciliature in ventral view, protargol impregnation, 165 μ m. The arrows mark the frontoterminal cirri.

Fig. 52 *Bakuella kreuzkampii* nov. spec. (from Mihailowitsch & Wilbert, 1990). Infraciliature in ventral view, protargol impregnation, 165 μ m. The arrows mark the frontoterminal cirri.

Fig. 53 *Paraurostyla pulchra* (from Buitkamp, 1977). Infraciliature in ventral view, protargol impregnation, 158 μ m.

Figs 54, 55 *Bakuella agamalievi* (from Agamaliev, 1972). 54 Infraciliature in ventral view, wet silver impregnation, 95 μ m. 55 Nucleus apparatus, Feulgen staining.



granules on entire surface, 2-4 granules near each cirrus, on dorsal surface oblique rows, 3-10 granules per row. Feeds on flagellates. Adoral zone of membranelles about 1/3 of body length. 3 frontal cirri, 8-10 buccal cirri, about 12 transverse cirri. 1 right marginal row. Frontoterminal cirri present. Locus classicus of *B. variabilis* is a temporary pool in a flooded agricultural field in Lee, New Hampshire, USA (70°58' W. Long., 43°8' N. Lat.).

Bakuella sp. in Wiackowski (1988) is not figured. Thus an identification is impossible.

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Figs 56, 57 *Bakuella variabilis* (56, from Borror, 1979; 57, from Borror & Wicklow, 1983). 56, 57 Infraciliature in ventral view, protargol impregnation and nigrosin-butanol staining, 270 μ m, 175 μ m. Right from Fig. 56 a middle morphogenetic stage.

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